WENLOCK STROPHEODONTIDAE (SILURIAN BRACHIOPODA) FROM THE WELSH BORDERLAND AND SOUTH WALES

by M. G. BASSETT

ABSTRACT. Eighteen species and subspecies of stropheodontid brachiopods are described from the Wenlock Series (Silurian) of the Welsh Borderland and South Wales, and are assigned to nine separate genera and subgenera. One new subgenus, Amphistrophia (Pembrostrophia), is recognized, together with the following new species and subspecies: Strophonella (Strophonella) euglypha gentilis, Amphistrophia (Pembrostrophia) freshwaterensis, Mclearnites coralli, and Pholidostrophia (Mesopholidostrophia) deflecta. Two separate stocks, represented by Leptostrophia (Eostropheodenta) and Amphistrophia (Pembrostrophia), are shown to retain dental plates into the Wenlock period.

ALTHOUGH the taxonomy and phylogenetic relationships of stropheodontid brachiopod genera have become fairly well established during the past thirty years, the recognition, interpretation, and nomenclature of British Wenlock species are still dependent largely on Davidson's Silurian Monograph (1866-71), in which all the strophomenid species were described in 1871. The purpose of the present paper is to systematically revise those stropheodontid species which occur in the Wenlock Series of the Welsh Borderland and South Wales in order to clarify their affinities with species from other areas and stratigraphical horizons. Material for this study has been collected mainly by the writer from the following areas: Wenlock Edge and Benthall Edge in Shropshire, Dudley and Walsall in the west English Midlands, the Ludlow Anticline, the Abberley and Malyern Hills, the inliers of May Hill, Woolhope, Usk, Tortworth, and Rumney (Cardiff), the Llandovery-Llandeilo district of Carmarthenshire, and sections at Freshwater East, Marloes Bay, and Winsle in Pembrokeshire. Supplementary collections have been studied in several museums in Britain, particularly the Davidson collection at the British Museum (Natural History) and the collections of the Geological Survey Museum, Institute of Geological Sciences.

Repositories. Throughout the text the repositories of type and figured specimens will be referred to by the following abbreviations: BM—British Museum (Natural History); GSM—Geological Survey Museum, Institute of Geological Sciences; NMW—National Museum of Wales, Cardiff; CMB—City Museum, Bristol; UB—University of Bristol Museum; SM—Sedgwick Museum, University of Cambridge; BU—Birmingham University (Geological Department Museum); NMI—National Museum of Ireland, Dublin; SMNH—Naturhistoriska Riksmuseet, Stockholm (Swedish Museum of Natural History); PMO—Paleontologisk Museum, Oslo.

In the Welsh Borderland the Wenlock Series comprises three formations, namely, in ascending order, the Woolhope Limestone, the Wenlock Shale, and the Wenlock Limestone. At Tortworth and throughout South Wales this tripartite division cannot

[Palaeontology, Vol. 14, Part 2, 1971, pp. 303-37, pls. 54-60.]

be recognized, the succession consisting instead of calcareous and sandy mudstones with thin limestone and sandstone horizons. The sequences throughout the area have recently been summarized elsewhere in tabular form (Bassett 1970, text-fig. 1) and their detailed correlation is currently being studied by the writer.

SYSTEMATIC DESCRIPTIONS

Order STROPHOMENIDA Öpik 1934 Superfamily STROPHOMENACEA King 1846 Family STROPHEODONTIDAE Caster 1939

The present supra-generic classification of the Stropheodontidae (Williams 1965, pp. H395-H403) is based mainly on the work of Caster (1939) and Williams (1953a). The latter author in 1953 established the use of subgenera to indicate the temporal relationships of evolving stropheodontid lineages and introduced the prefixes 'Eo', 'Meso', and 'Talaeo' to denote early, mature, and late stages respectively. As more material is being examined in detail it is becoming evident that although the generally accepted picture of stropheodontid phylogeny still holds broadly true, the changes that take place in lineages of this type are not direct, and that early but conservative members of a stock may coexist for some time with their immediate descendants. For example Cocks (1967) showed that in the Upper Llandovery a number of forms with dental plates ('Eo' stage) may exist contemporaneously with direct descendants which lack dental plates ('Meso' stage). The same type of relationship can now be demonstrated with some of the Wenlock genera described below, and although Williams (1953a, p. 9) and text-fig. 4) considered that dental plates were lost in stropheodontids by the end of Llandovery times, at least two separate stocks can be shown to retain these structures well into the Wenlock period.

Subfamily STROPHEODONTINAE Caster 1939 Genus Brachyprion Shaler 1865

Type species. Strophomena leda Billings 1860, by original designation of Shaler 1865, p. 63.

Williams (1953a, p. 35; 1965, p. H395) regarded *Brachyprion* as a subgenus of *Strophodonta*, whereas both Cocks (1967, p. 256) and Havlíček (1967, p. 139) described it as an independent genus. The relatively gently concavo-convex lateral profile, and the configuration of the non-flabellate ventral muscle field in *Brachyprion* together indicate an affinity with the leptostrophiid stock, and the work of Cocks (1967, p. 258) suggests that it may have been derived from *Leptostrophia* s.s. in Middle or early Upper Llandovery times. In contrast, *Strophodonta* has a fairly strongly concavo-convex lateral profile and a large, well impressed, flabellate ventral muscle field, features which are together suggestive of a close relationship with the megastrophiids. These postulated differences in the relationships of *Brachyprion* and *Strophodonta* are here considered sufficient to warrant their recognition as separate genera, but *Brachyprion* is retained as an early member of the Stropheodontinae, pending an investigation of its constituent species.

Brachyprion waltonii (Davidson)

Plate 54, figs, 1-5

1848	Leptaena waltonii Davidson, p. 317, pl. 3, fig. 6.
1866	Leptaena waltoni Davidson; Davidson, pl. 8, fig. 19.
1871	Strophomena waltoni (Davidson); Davidson, p. 310, pl. 42, fig. 11.
1956	Strophomena waltoni (Davidson); Curtis, p. 150.
1967	Brachyprion waltoni (Davidson); Cocks, p. 256.

Description. Exterior. Gently to moderately concavo-convex with subquadrate outline. Hinge-line straight, cardinal angles obtusely rounded. Point of maximum width commonly at about mid-length of shell. Lateral margins gently curved, anterior margin evenly rounded or sub-parallel to hinge. Anterior commissure rectimarginate.

Ventral interarea plane, apsacline, 2 to 3 times as long as dorsal interarea. Presence or absence of pseudodeltidium not apparent on material available. Delthyrial angle about 80°. Dorsal interarea short, anacline. Notothyrium sealed by massive, convex chilidium which extends up into delthyrium.

Radial ornament equally to subequally parvicostellate with an average of 4 costellae per mm over whole surface of shell. Costellae are low, rounded, and radiate from umbo with little curvature. Very fine, closely spaced growth fila are visible on well-preserved specimens.

Interior of pedicle valve. Ventral process low, produced anteriorly as slender myophragm which longitudinally bisects muscle field. Extent of denticulation of hinge not observed. Muscle field broadly triangular in outline, moderately well impressed, confined to posterior half of valve, bounded laterally by pair of low ridges which are anterolaterally divergent at about 80–90° to one another. Fairly coarse pseudopunctae cover interior surface of valve, apart from muscle field.

Interior of brachial valve. Unknown.

Dimensions of figured specimens in mm		Length	Maximum width	Hinge width
Complete shell	Holotype, BM B5989	18.9	22.3	18.0
Complete shell	UB 12325-1	19.4	21.0	18.3
Partially exfoliated exterior of pedicle valve	UB 12325-2	19.5	22.6	19.0 est.
Partially exfoliated exterior of pedicle valve	GSM DEW9625	16.4	19.6	16.1
Impression of exfoliated pedicle valve	GSM DEW9627	_		

Holotype (by monotypy). BM B5989, from the 'Wenlock Shale, Falfield', Tortworth inlier, Glos. This is the specimen that was originally figured by Davidson (1848, pl. 3, fig. 6) and later refigured by him (1866, pl. 8, fig. 19; 1871, pl. 42, fig. 11). It is refigured on Plate 54, figs. $1\,a$ –c. The Wenlock Shale horizon at Falfield probably refers to the *Pycnactis* band which immediately overlies the limestone band at the base of the Wenlock Series (Curtis 1955, p. 6; 1956, p. 152).

The holotype of *B. waltonii* is rather unusual in that it has attached to it the 3 syntype specimens of the inarticulate brachiopod '*Crania*' siluriana Davidson 1866, p. 82, plate 8, figs. 19, 20. These 3 specimens bear a separate registration number (BM 15034–6).

Remarks. In synonymy lists of this species Davidson twice (1848, p. 317; 1871, p. 310) referred to Leptaena waltonii Davidson as being published in the London Geological

Journal for 1847, plate 26, fig. 3. However, plate 26 was never published in that issue of the journal and the first description and figure of *L. waltonii* were not published by Davidson until 1848. The original spelling of the specific name was *waltonii*, although in later papers Davidson and other authors used only a single *i* (see synonymy). Recommendation 31A of the International Code of Zoological Nomenclature (1964) states that there is no mandatory spelling for specific names based on modern personal names, although the single *i* is preferred. It is now usual to keep the double *i* in those names originally spelt in that way but to use the single *i* for new names. The original spelling of *waltonii* should therefore be maintained.

Distribution. B. waltonii is known only from the Tortworth inlier, Gloucestershire. As noted above the holotype is probably from the *Pycnactis* band which immediately overlies the limestone band at the base of the Wenlock Series; all other specimens examined by the writer are from the basal limestone of Brinkmarsh Quarry, 400 yd NNW of Brinkmarsh Farm, Whitfield (Grid Ref. ST 6735.9130).

Brachyprion sp.

Plate 54, figs. 6-8

Comparison. Brachyprion sp. is distinguished from B. waltonii chiefly by its unequally parvicostellate ornament and relatively wider hinge-line, which commonly forms the point of maximum width of the shell. In B. waltonii the ornament is equally to subequally parvicostellate and the point of maximum width is near to the mid-length.

EXPLANATION OF PLATE 54

Figs. 1-5. Brachyprion waltonii (Davidson).

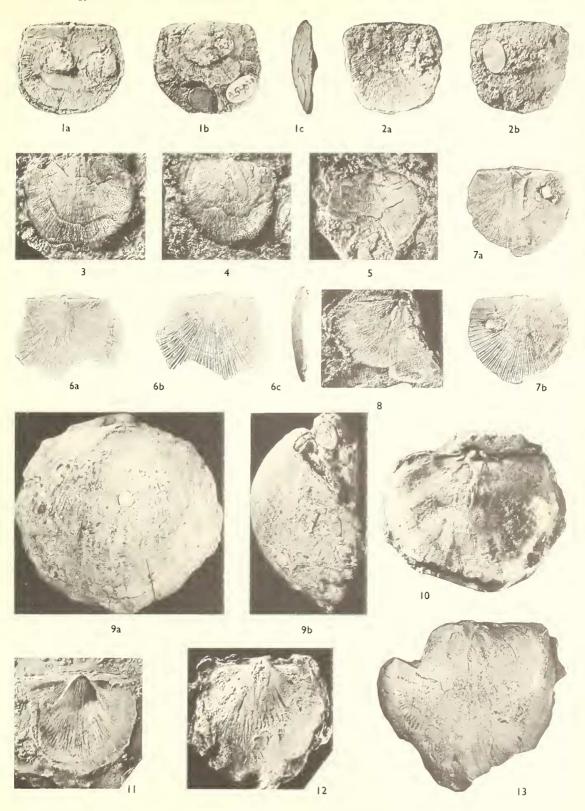
1 a-c. Dorsal, ventral, and lateral views of complete shell, holotype, BM B5989, $\times 1.3$, 'Wenlock Shale' (probably *Pycnactis* band), Falfield, Tortworth inlier, Glos.

2a, b. Dorsal and ventral views of complete shell, UB 12325–1, ×1·3, basal Wenlock (*Pycnactis* band or basal limestone band), Brinkmarsh Quarry, Whitfield, Tortworth inlier, Glos., ST/6735. 9130.

- 3, 4. Partially exfoliated exterior of pedicle valve; 3, UB 12325–2; 4, GSM DEW9625, ×1·3, basal limestone of Wenlock Series, locality as for fig. 2.
- 5. Impression of exfoliated pedicle valve, GSM DEW9627, $\times 1.3$, basal limestone of Wenlock Series, locality as for fig. 2.
- Figs. 6–8. *Brachyprion* sp. Wenlock Shale, railway cutting, Daw End, Walsall, Staffs., SK/0360.0030. 6*a–c*. Dorsal, ventral, and lateral views of broken shell, NMW 70.3G.1, ×1·3.

7a, b. Dorsal and ventral views of broken shell, NMW 70.3G.2, $\times 1.3$.

- 8. Artificially produced (calcined) internal mould of brachial valve, NMW 70.3G.3a, $\times 1.3$, from approx. 200 ft below Wenlock Limestone.
- Figs. 9-13. Megastrophia (Protomegastrophia) semiglobosa (Davidson).
 - 9a, b. Ventral and lateral views of pedicle valve, lectotype, BM B13642, $\times 1$, Wenlock Shale or Limestone, Rushall Canal, near Walsall, Staffs.
 - 10, 13. Interiors of brachial valves; 10, BM B45075; 13, BM 746 ×1, Wenlock Limestone, Dudley, Worcs.
 - 11. Interior of pedicle valve, BM BB6419, ×1, Wenlock Limestone, Dudley, Worcs.
 - 12. Internal mould of pedicle valve, GSM 12758, ×1, Wenlock Shale, Usk inlier, Mon.



BASSETT, Wenlock Stropheodontidae



The following description of *Brachyprion* sp. is based on a collection of 18 incomplete articulated specimens, a number of which have been roasted in a Bunsen flame and the calcined shell material scraped away to produce artificial internal moulds. The detail that can be observed in preparations of this type is rather limited and while an assignment to *Brachyprion* is possible, based on the convexity of the valves, the musculature, and the nature of the ornament, specific determination is not thought advisable until more material becomes available and related species can be compared in detail.

Description. Exterior. Shell thin, gently concavo-convex, body cavity narrow. Sub-quadrate to semicircular in outline with maximum width commonly at straight hingeline, which may be produced as short, rounded ears. Lateral and anterior margins evenly curved; anterior commissure rectimarginate.

Ventral interarea plane to very gently concave, apsacline, 4–5 times as long as dorsal interarea, which is plane, anacline. Median third of both interareas bears fine ridges caused by impress of internal denticulation. Delthyrial angle about 80°. Pseudodeltidium small, gently convex; chilidium massive, convex, completely sealing notothyrium and extending up into delthyrium.

Ornament unequally parvicostellate with up to 4 fine costellae occupying interspaces between larger, rounded costellae. There are 4–5 costellae per mm at the 5-mm growth stage of pedicle valve. Costellae increase in strength anteriorly, are straight along midline of shell and curve gently on flanks. Whole surface is crossed by extremely fine, concentric growth fila.

Interior of pedicle valve. Pseudodeltidium supported by low, short ventral process, gently concave along its mid-length and extending anteriorly into shallow, narrow, rounded groove bisecting muscle field. Process pits small, shallow. Muscle field broadly triangular in outline, occupying about one-third of valve length and up to one-third width. Muscle field unbounded anteriorly but may be bounded laterally by low ridges. Adductor scars narrow, elongate, situated adjacent to median groove and confined to posterior half of muscle field. Diductor scars large, sub-triangular, enclosing adductor scars laterally and anteriorly.

Iuterior of brachial valve. Cardinal process lobes narrow, platelike, initially divergent at about 160° to one another but curving anteriorly to be finally divergent at about 90°. Socket ridges well developed, antero-laterally divergent at about 100° to one another. Notothyrial platform low, hollowed out immediately below cardinal process lobes and produced anteriorly as low, convex ridge which longitudinally bisects muscle field.

Muscle field subquadrate, well impressed, occupying about one-third of valve length and one-quarter width; laterally bounded by broad, high, slightly curved ridges, but remains unbounded anteriorly. Pair of lanceolate scars lies alongside median ridge, enclosed by larger, more deeply impressed pair of scars with sub-oval outline.

Internal surface of both valves covered with fine, radially aligned pseudopunctae, and shows impress of external ornament.

Distribution. Brachyprion sp. is known only from the Wenlock Shale of the railway cutting at Daw End, Walsall, Staffordshire (Grid Ref. SK 0360.0030).

Genus MEGASTROPHIA Caster 1939 Subgenus Megastrophia (Protomegastrophia) Caster 1939

Type species. Leptaena profunda Hall 1852, by original designation of Caster 1939, p. 28.

Megastrophia (Protomegastrophia) semiglobosa (Davidson)

Plate 54, figs. 9-13; Plate 55, figs. 1-3

- 1847 Leptaena imbrex (Pander); Davidson, p. 55, pl. 12, figs. 25–8; non Pander 1830.
- 1848 Leptaena imbrex (Pander); Davidson, p. 318, pl. 3, fig. 8; non Pander 1830.
- 1854 Strophomena imbrex (Pander) Salter in Murchison, table on p. 488, woodcut 41, p. 224, figs. 6, 7; non Pander 1830.
- 1871 Strophomena imbrex (Pander) var. semiglobosa Davidson, p. 286, pars, pl. 41, figs. 1-4, non figs. 5, 6.
- 1883 Strophomena imbrex var. semiglobosa Davidson; Davidson, p. 195.
- 1953a Megastrophia semiglobosa (Davidson): Williams, p. 21.

Comparison. Cocks (1967, p. 260) erected a new subgenus, Eomegastrophia, to include megastrophiids which possess dental plates. The type of this subgenus is M. (E.) ethica Cocks from the Upper Llandovery of Shropshire and is probably directly ancestral to the Wenlock species described here. While the two species are closely related in details of musculature, ornament, and convexity, M. (P.) semiglobosa may easily be distinguished by the absence of dental plates. The Scottish Ordovician specimens figured by Davidson (1871, pl. 41, figs. 5, 6) are not stropheodontids; they belong to Dactylogonia? semiglobosina (Davidson) (see Davidson 1883, pp. 195-6; Williams 1962, pp. 201-2).

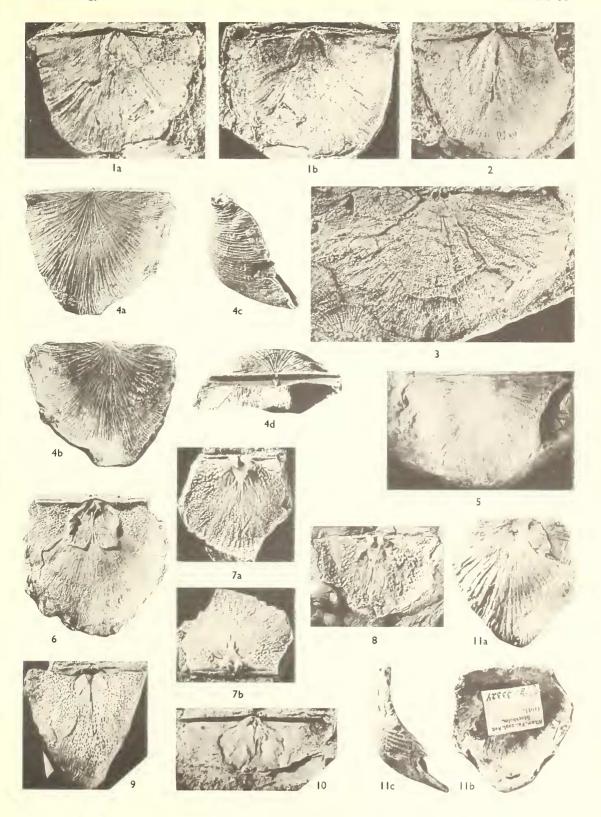
EXPLANATION OF PLATE 55

Figs. 1-3. Megastrophia (Protomegastrophia) semiglobosa (Davidson).

- 1a, b. Internal mould of pedicle valve and latex cast, NMW 70.3G.4, \times 1, Wenlock Shale, exposures below tumuli on Craig-y-Garcyd, 320 yd NW of Hen-rhiw Farm, Usk inlier, Mon., SO/3570.0275.
- 2. Internal mould of pedicle valve, GSM 12756, ×1, Wenlock Shale, Usk inlier, Mon.
- 3. Internal mould of brachial valve, GSM HC991, ×1, late Wenlock mudstone, old overflow trench near Middleton Hall, Carms., SN/5265.1879.

Figs. 4-11. Strophonella (Strophonella) euglypha (Dalman).

- 4a-d. Dorsal, ventral, lateral and posterior views of complete shell, BU 405 (ex Ketley collection), $\times 1$, Wenlock Limestone, Dudley, Worcs.
- 5. Exterior of brachial valve, SMNH Br2342, lectotype, ×1, Mulde Marl, Djupvik, Gotland.
- 6. Interior of pedicle valve, BU 406 (ex Ketley collection), ×1, Wenlock Limestone, Dudley, Worcs.
- 7a, b. Dorsal and posterior views of interior of brachial valve, BM BB32805 (ex B5675), $\times 1$, Wenlock Limestone, Dudley, Worcs.
- 8. Interior of brachial valve, BU 407 (ex Ketley collection), ×1, Wenlock Limestone, Dudley, Worcs.
- 9. Internal mould of brachial valve, GSM 13369, \times 1, Aymestry Limestone (Ludlow Series), Dormington Wood, probably Woolhope inlier, Herefordshire.
- 10. Internal mould of pedicle valve, NMW 70.3G.5a, ×1, siltstone overlying Wenlock Limestone, old quarry at Cwm, Usk inlier, Mon., SO/3331.0160.
- $11 \, a$ -c. Dorsal, ventral, and lateral views of complete shell, SMNH Br33324, $\times 1$, Gotland, probably Mulde Marl. Djupvik.



BASSETT, Wenlock Stropheodontidae



Description. Exterior. Fairly large, thick shells, moderately to strongly concavoconvex, sometimes flattened slightly towards cardinal extremities. Outline subcircular with maximum width at any point between hinge and mid-length of shell. Hinge-line straight, commonly produced as short, rounded ears. Lateral margins commonly evenly curved, but may show slight constriction immediately anterior to hinge. Commissures smooth, anterior commissure rectimarginate.

Ventral interarea plane, apsacline, up to 3 times as long as dorsal interarea. Delthyrial angle varies from about 80–100°. Pseudodeltidium small, apical, gently convex. Dorsal interarea plane, anacline. Notothyrium closed by massive, convex chilidium which extends up into delthyrium.

Ornament unequally parvicostellate. Up to 8 fine, threadlike costellae occupy broad interspaces between stronger, rounded costellae. Costellae fairly straight, about 4 or 5 per mm at 5-mm growth stage of pedicle valve.

Interior of pedicle valve. Ventral process low, gently concave along its mid-length, produced anteriorly as slender myophragm. Anteriorly, myophragm decreases in height and width and in some specimens passes into shallow groove. Process pits shallow. Hinge-line denticulate for up to one-third of its length, denticles being borne on pair of low denticular plates.

Muscle field broadly triangular in outline, becoming flabellate anteriorly. Bounding ridges low or absent. Adductor scars small, narrow, lanceolate, situated in centre of muscle field and separated by myophragm; bounded laterally and anteriorly by large, sub-oval diductor scars. Area immediately lateral to muscle field may be coarsely pustulose, and whole of internal surface of valve bears fairly coarse pseudopunctae.

Interior of brachial valve. Cardinalia are supported on broad, low notothyrial platform which is deeply hollowed out below cardinal process lobes; these lobes consist of a pair of stout, upright plates with attachment faces directed postero-laterally, and are separated by rounded groove bearing low, triangular ridge. Socket plates weak, flat, widely divergent antero-laterally, with crenulations on their posterior faces.

Muscle field elongate—oval in outline, consisting of 2 oval adductor scars separated by prominent myophragm which narrows anteriorly. Muscle field occupies up to one-third of valve width and up to one-half length.

Median third of hinge bears denticles complementary to those of pedicle valve.

Dimensions of figured specimens in mm

	Length	Width
Lectotype, BM B13642	51.5	
BM BB6419	26.0	32.8
GSM 12756	24.8	33.6 est.
GSM 12758	34·0 est.	_
BM B746	42.6	45.6
BM B45075	38.7	42.9
NMW 70.3G.4	33.4	45.0
GSM HC991	38.5	
	BM BB6419 GSM 12756 GSM 12758 BM B746 BM B45075 NMW 70.3G.4	Lectotype, BM B13642 51.5 BM BB6419 26.0 GSM 12756 24.8 GSM 12758 34.0 est. BM B746 42.6 BM B45075 38.7 NMW 70.3G.4 33.4

Lectotype (here selected): BM B13642 (figured Davidson 1871, pl. 41, fig. 2). This is one of 4 specimens in the Davidson collection which are mounted on a card bearing Davidson's handwriting and identifying the specimens as types. The other 3 specimens cannot be identified with certainty with Davidson's

figures, which were often composite, but his plate 41, figs. 1a-b, are possibly based on the same collection. The card in Davidson's handwriting states that the types are from the Wenlock Limestone of Walsall and Dudley. According to the plate legend, however, the lectotype is from the Wenlock Shale of Rushall Canal, near Walsall; its exact horizon is therefore in some doubt. The lectotype is refigured in Plate 54, figs. 9a, b.

Distribution. This species does not occur very commonly in present Wenlock outcrops but numerous specimens have been examined in museum collections from the Wenlock Shale and Limestone of Walsall and Dudley. It has been collected by the writer from the Wenlock Shale of the Usk inlier, the late Wenlock mudstones of the Rumney (Cardiff) inlier and the late Wenlock mudstones of the Llandeilo district, Carmarthenshire. It is not known with certainty from early Wenlock horizons and has not been found in Pembrokeshire.

Genus Strophonella (Eostrophonella) Williams 1950

Type species. Amplistrophia davidsoni Holtedahl 1916, by original designation of Williams 1950, p. 281.

Discussion. No Wenlock species of Strophonella (Eostrophonella) are known, the subgenus being recorded only from the Llandovery Series (e.g. see Williams 1951, p. 127). It is discussed here, however, since during the course of this work it became necessary to clarify the affinities of the poorly known species 'Strophomena' simulans McCoy 1851; examination of the type specimens of simulans reveals that the original description was based on poorly preserved material containing, among others, a specimen of Strophonella (Eostrophonella) of probable Lower Llandovery age, and a specimen of Strophonella (Strophonella) from the Wenlock Series. The Wenlock specimen is redescribed in this paper as S. (Strophonella) euglypha gentilis subsp. nov. (see p. 313) and the specific name simulans is retained for the specimen of S. (Eostrophonella). The relationships of these specimens are discussed in full on p. 314 following the description of S. (S.) euglypha gentilis.

Subgenus Strophonella (Strophonella) Hall 1879

Type species. Strophomena semifasciata Hall 1863, by subsequent designation of Hall and Clarke 1892, p. 291.

Strophonella (Strophonella) euglypha (Dalman)

Plate 55, figs. 4-11; Plate 56, figs. 1, 2

- 1828 Leptaena englypha Dalman, p. 108, pl. 1, fig. 3a, c, non fig. 3b.
- 1828 Leptaena euglypha Dalman; Hisinger, pl. 4, figs. 7a, b.
- 1839 Leptaena euglypha Dalman; J. de C. Sowerby in Murchison, p. 622, pl. 12, fig. 1.
- 1847 Leptaena englypha Dalman; Davidson, p. 56, pl. 12, figs. 1-4.
- 1848 Leptaena englypha Dalman; Davidson, p. 316, pl. 3, fig. 4.
- 1852 Leptaena (Strophomena) englypha (Dalman); McCoy, p. 243.
- 1861 Strophomena euglypha (Dalman); Lindström, p. 372.
- 1871 Strophomena englypha (Hisinger); Davidson, p. 288, pars pl. 40, figs. 1–3, non figs. 4, 5.
- ? 1916 Strophonella englypha (Hisinger); Holtedahl, p. 66, pl. 6, figs. 5, 6.

1953a Strophonella euglypha (Hisinger); Williams, p. 21.

1963 Strophonella euglypha (Hisinger); Holland et al., pl. 3, figs. 8, 9.

? 1967 Strophonella euglypha (Hisinger); Havlíček, p. 180, pl. 37, figs. 6-8; pl. 50, figs. 5, 8, 9.

Comparison. Williams (1951, p. 128) showed that two of the specimens figured by Davidson in 1871 (pl. 40, figs. 4, 5) as 'Strophomena' euglypha belong to Strophonella (Eostrophonella) davidsoni (Holtedahl). This Llandovery species differs from S. (S.) euglypha in having short dental plates in the interior of the pedicle valve and in having a less prominent, more rounded ventral muscle field.

Description. Exterior. Pedicle valve initially gently convex; brachial valve initially plane to weakly concave. At length of about 13–20 mm valves become resupinate and develop strong convexi-concave profile. Outline semicircular to subtriangular, varying from as wide as long to about seven-tenths as long as wide. Maximum width at or slightly posterior to straight hinge-line, which in well-preserved shells is produced as short, rounded ears. Margins of shell commonly evenly curved but anterior margin may be extended anteriorly as tongue-like trail to give an overall subtriangular outline. Commissures smooth, anterior commissure rectimarginate.

Ventral interarea plane, apsacline, 2–3 times as long as dorsal interarea. Delthyrial angle about 40°. Delthyrium almost completely closed by well-developed, convex pseudodeltidium. Dorsal interarea linear, plane, anacline. Chilidium strong, convex, completely sealing notothyrium. Both interareas show traces of internal denticulation.

Ornament unequally parvicostellate with up to 6 (commonly 2 or 3) very fine capillae occupying wide interspaces between major rounded costellae. At 10-mm growth stage there are 4–5 costellae per mm. Very fine, closely spaced, concentric growth fila may be seen on well-preserved shells. A number of specimens exhibit fine crenulations of shell along posterior margin, inclined obliquely to hinge (e.g. see Pl. 55, figs. 4a, b).

Interior of pedicle valve. Pseudodeltidium supported by stout, hastate, ventral process, hollowed out along its mid-length, and produced anteriorly as strong, rounded myophragm. Deep process pits laterally bound ventral process. Dental plates absent. Median third of hinge bears pair of well-developed denticular plates.

Muscle field strongly impressed, subquadrate, flabellate, occupying about one-third of width of valve and up to one-half length. Strong muscle bounding ridges arise immediately anterior to hinge, diverging initially at about 90° to one another, then becoming parallel and finally turning medially and posteriorly to intersect myophragm slightly posterior to its anterior extremity. Adductor scars narrow, lanceolate, situated adjacent to myophragm and surrounded by larger, oval diductor scars.

Extra-muscular area shows traces of external ornament and may be coarsely pustulose.

Interior of brachial valve. Cardinalia raised on broad notothyrial platform, produced anteriorly as convex median ridge. Cardinal process lobes stout, pear-shaped, divergent, grooved along their mid-length, with attachment faces directed postero-ventrally. Sockets shallow, socket plates short, strong, antero-laterally divergent at about 110° to one another.

Muscle field moderately well impressed, truncated oval in outline, occupying about one-quarter of valve width and commonly about two-thirds as long as wide. Low,

broad, slightly curved ridges may bound muscle field laterally but it is unbounded anteriorly and bisected longitudinally by median ridge which tapers anteriorly.

Internal surface may be coarsely tuberculate, especially immediately lateral to muscle field.

Dimensions of figured specimens in mm

		Length	Width
Exterior of brachial valve	Lectotype, SMNH Br2342	28.5	45·0 est.
Complete shell	SMNH Br33324	35.0	_
Interior of pedicle valve	SMNH Br33301	29.1	_
Complete shell	BU 405 (ex Ketley collection)	35.6	40.5
Interior of pedicle valve	BU 406 (ex Ketley collection)	36.4	38.1
Interior of pedicle valve	BU Holcroft Collection no. 297	39.6	40.5
Interior of brachial valve	BU 407 (ex Ketley collection)	_	34.9
Interior of brachial valve	BM BB32805 (ex B5675)	_	
Internal mould of brachial valve	GSM 13369	35.8	32.5 est.
Internal mould of pedicle valve	NMW 70.3G.5a		41.3

Type and figured specimens. Lectotype (here selected): the specimen figured by Dalman 1828, plate 1, fig. 3a, now housed in the Department of Palaeozoology, Swedish Museum of Natural History, Stockholm (Br2342, Hisinger sample 472). This specimen, from the Mulde Marl of Djupvik, Gotland is refigured on Plate 55, fig. 8. The Mulde Marl is regarded as being of late Wenlock age (Hede 1960, p. 49). The specimen figured by Dalman 1828, plate 1, fig. 3b (SMNH Br2336, Hisinger sample 473) does not belong to S. euglypha but to the genus Megastrophia. Examination of the lectotype and possible topotype material of S. englypha leaves no doubt that the British and Swedish shells are conspecific.

Remarks. The authorship of this well-known species has been the subject of some confusion in the past (see synonymy), being referred by various authors to either Dalman

EXPLANATION OF PLATE 56

Figs. 1, 2. Strophonella (Strophonella) englypha (Dalman).

- 1. Interior of pedicle valve, BU Holcroft collection no. 297, ×1, 'Upper Silurian' (probably Wenlock Limestone), Wren's Nest, Dudley, Worcs.
- 2, Interior of pedicle valve, SMNH Br33301, ×1, Gotland, probably Mulde Marl, Djupyik,

Figs. 3-6. Strophonella (Strophonella) englypha gentilis subsp. nov.

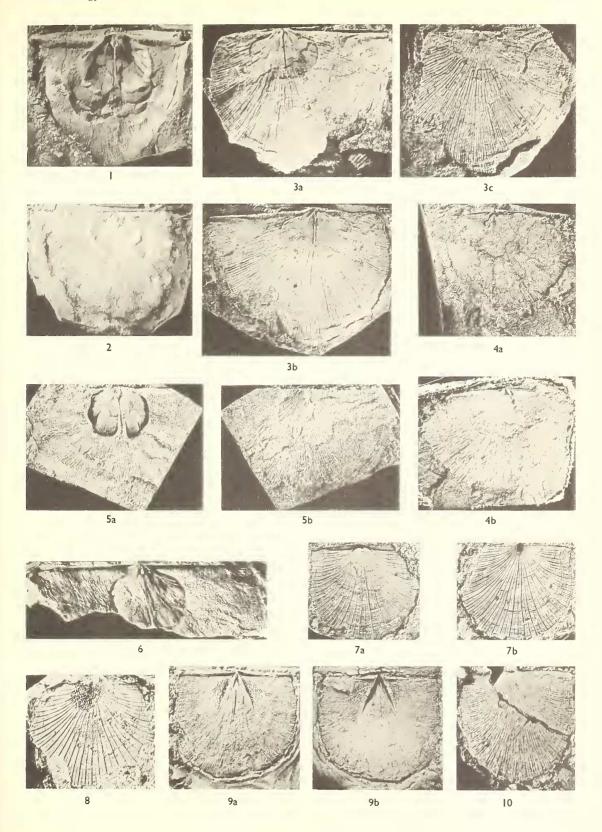
- 3 a–c. Internal mould of pedicle valve, latex cast, and counterpart external mould, holotype, NMW 70.3G.6a, b, \times 1, late Wenlock mudstone, forestry track section, W side of Sawdde gorge, Carms., SN/7200.2525.
- 4a, b. Internal mould of brachial valve and latex cast, NMW 70.3G.24a, $\times 1$, locality and horizon as for fig. 3.
- 5a, b. Internal mould of pedicle valve and counterpart external mould, SM A10272a, b, $\times 1$, Wenlock Series, Middleton Park, Carms.
- 6. Internal mould of pedicle valve, GSM DEX2853, ×1, late Wenlock mudstone, old overflow trench near Middleton Hall, Carms., SN/5265.1879.

Figs. 7, 8. Leptostrophia (Eostropheodonta) sp.

- 7a, b. Internal mould of pedicle valve and counterpart external mould, NMW 70.3G.11a, b, \times 1·3, Wenlock Shale, exposures below tumuli on Craig-y-Garcyd, 320 yd NW of Hen-rhiw Farm, Usk inlier, Mon., SO/3570.0275.
- 8. External mould of pedicle valve, NMW 70.3G.12a, ×1·3, locality and horizon as for fig. 7.

Figs. 9-10. Leptostrophia (Leptostrophia) filosa (J. de C. Sowerby).

- 9a, b. Internal mould of pedicle valve and latex cast, NMW 70.3G.9a, $\times 1.3$, siltstone overlying Wenlock Limestone, old quarry at Cwm, Usk inlier, Mon., SO/3331.0160.
- 10. Exterior of pedicle valve, GSM 13307, $\times 1.3$, Wenlock Limestone, Usk inlier, Mon.; figured Davidson 1871, pl. 44, fig. 16.



BASSETT, Wenlock Stropheodontidae



or Hisinger and even to Sowerby by Davidson (1871, pl. 40) in his plate legend. Dr. V. Jaanusson has kindly supplied the writer with information to help to clarify the matter. Davidson's reference (1871, p. 288) to Leptaena euglypha Hisinger 1819 is certainly a mistake since the species is neither mentioned nor figured in Hisinger's paper of that year. The species name Leptaena euglypha was first published in the same year (1828) by both Dalman and Hisinger, though it is not known which publication has priority. However, it seems best to refer the species to Dalman since Hisinger does so and since Dalman does not mention Hisinger's authorship. The problem now is whether the author should be regarded as Dalman 1828 or Dalman in Hisinger 1828. This depends on which of the publications has priority and there may be a question of priority of days. Fortunately this is a purely academic matter because the description of the species in both papers is based on the same material and thus selection of the lectotype from the specimens figured by Dalman satisfies the nomenclatural requirement of both papers.

Distribution. S. (S.) euglypha is widespread in the Wenlock of the Welsh Borderland, occurring most commonly in the Wenlock Limestone and less commonly in the upper calcareous horizons of the Wenlock Shale. It is unknown to the writer from low in the Wenlock Shale but a single specimen is recorded from the Woolhope Limestone in the Geological Survey collections (GSM 12679). The species is also found in late Wenlock mudstones and sandstones at Tortworth and Rumney (Cardiff). In the Llandovery-Llandeilo district, Carmarthenshire, S. (S.) euglypha s.s. appears to be replaced by S (S.) euglypha gentilis (see below); neither subspecies is known from Pembrokeshire.

Lawson (1960, p. 117) recorded *S. euglypha* as rare or absent in Britain after Bringewoodian times, while in Gotland it was recorded by Hede (1960) from localities in the Mulde Marl (late Wenlock) and from the Hemse group (early Ludlow). Holtedahl (1916, p. 66) and Havilíček (1967, p. 180) recorded *S. euglypha* from Norway and Czechoslovakia respectively, though these identifications have not been checked. The full recorded range of the species is from early Wenlock to Ludlow (Bringewoodian).

Strophonella (Strophonella) euglypha (Dalman) gentilis subsp. nov.

Plate 56, figs. 3-6

- 1851 Strophomena simulans McCoy, p. 403, pars.
- 1852 Strophomena simulans McCoy; McCoy in Sedgwick and McCoy, p. 246 pars, pl. 1H, fig. 35, non figs. 33, 34.
- 1871 Strophomena simulans McCoy; Davidson, p. 297, pars, pl. 42, fig. 10, non figs, 9, 9 a-c.

Discussion. Specimens of Strophonella that have been collected from the late Wenlock mudstones and siltstones of the Llandeilo district, Carmarthenshire, are closely similar in outline and ornament to S. (S.) euglypha from the more calcareous horizons of the Welsh Borderland. The South Wales specimens may, however, be distinguished by having a more rounded ventral muscle field, a less-strongly impressed dorsal muscle field, and by being relatively broader and more gently resupinate than is typical of S. (S.) euglypha s.s. These differences are probably due largely to the more clastic environment in the South Wales area, but the specimens are sufficiently distinct to warrant their recognition as a new subspecies within S. (S.) euglypha.

Dimensions of figured specimens in mm

		Length	Width
Internal mould of pedicle valve and counterpart			
external mould	Holotype, NMW 70.3G.6 a, b	38.3	60.0 est.
Internal mould of brachial valve	NMW 70.3G.24a		
Internal mould of pedicle valve and counter-			
part external mould	SM A10272 a, b		
Internal mould of pedicle valve	GSM DEX2853	_	60.8

Type and figured specimens. Holotype, NMW 70.3G.6a, b, the internal mould of a pedicle valve and its counterpart external mould, figured on Plate 56, figs. 3a-c. The other specimens whose dimensions are given above are paratypes. One of these (SM A10272a, b) was included by McCoy and Davidson (see synonymy) in 'Strophomena' simulans McCoy, but as the lectotype of simulans is a specimen of Strophonella (Eostrophonella), of probable Lower Llandovery age (see discussion below), the Wenlock specimen of Strophonella (Strophonella) is re-assigned here to the new subspecies gentilis.

Distribution. S. (S.) euglypha gentilis occurs fairly commonly in the late Wenlock mudstones of the forestry track section along the west bank of the Sawdde gorge, Carmarthenshire (Grid Ref. SN/7200.2525) where it is associated with the graptolite *Monograptus flemingii flemingii* Salter. It has also been found in sandy siltstones of Wenlock age in an old overflow trench near Middleton Hall, Carmarthenshire (Grid. Ref. SO/5265.1879). Large strophonellids collected from comparable horizons throughout the Llandeilo district are generally broken, but almost certainly belong to this subspecies.

Discussion. As discussed both immediately above and earlier (p. 310), McCoy's original description (1851, p. 403) of *Strophomena simulans* was based on a number of specimens now known to belong to different species. The same specimens were later figured by McCoy (1852, pl. 1H, figs. 33–35) and by Davidson (1871, pl. 42, figs. 9, 10). All the material is now in the Sedgwick Museum, Cambridge, and in order to clarify their relationships, each specimen is discussed separately.

1. SM A42416a, b. Internal mould of pedicle valve and counterpart external mould. Here selected as lectotype of *Strophomena simulans* and identified as a species of *Strophomella* (*Eostrophomella*). A42416a was figured by McCoy 1852, plate 1H, fig. 34 and in the reconstruction of fig. 34a. The specimens are from Cefn Coch, Glyn Ceiriog, Denbighshire ('Upper Bala' of McCoy); the locality suggests that they were from the Fron Frys Slates, of probable Lower Llandovery age (Groom and Lake 1908, p. 553, pl. 53; Curtis in Whittard 1961, p. 92).

2. SM A42417. Internal mould of pedicle valve of an indeterminate resupinate strophomenid, possibly a species of *Amphistrophia*. Used in the reconstruction of McCoy 1852, plate 1H, figs. 33, 34a. This specimen is from Blain y Cwm, west of Nantyre, Glyn Ceiriog, Denbighshire ('Upper Bala' schists

of McCov): the exact horizon is unknown.

3. SM A45163. External mould of brachial valve of a strophomenid, possibly *Megastrophia (Protomegastrophia) semiglobosa* (Davidson). Probably used to complete the restoration of McCoy 1852, plate 1H, figs. 33, 34a. The specimen is from McCoy's 'Upper Bala', Golden Grove, Llandeilo, Carmarthenshire; the locality is suggestive of a Wenlock age, a conclusion that is supported by the lithology and by the presence in the same slab of an eospiriferid, probably *Cyrtia exporrecta* (Wahlenberg).

4. SM A10272a, b. Internal mould of pedicle valve and counterpart external mould. This is the specimen identified and figured (Pl. 56, figs. 5a, b) as S. (S.) euglypha gentilis; it was figured by McCoy 1852, plate 1H, fig. 35. It is the specimen referred to by McCoy (1851, p. 404; 1852, p. 246) as 'one doubtful specimen in the sandy schists of the Malverns, Worcestershire'. The locality is almost certainly a mistake, since both Salter (1873, p. 147) and Woods (1891, p. 64) indicated that it was collected

from the Wenlock of Middleton Park, Carmarthenshire. The lithology of the specimen compares closely with that in material collected by the writer from localities in Middleton Park, while neither the subspecies nor similar lithological types have been identified in numerous collections from the Malverns.

Subfamily LEPTOSTROPHIINAE Caster 1939 Genus LEPTOSTROPHIA Hall and Clarke 1892 Subgenus Leptostrophia (Leptostrophia) Hall and Clarke 1892

Type species. Stropheodonta magnifica Hall 1857, by original designation of Hall and Clarke 1892, p. 288.

Leptostrophia (Leptostrophia) filosa (J. de C. Sowerby)

Plate 56, figs. 9, 10; Plate 57, figs. 1-6

- 1839 Orthis filosa J. de C. Sowerby in Murchison, p. 630, pl. 13, fig. 12.
- 1847 Orthis filosa J. de C. Sowerby; Davidson, p. 62, pl. 13, fig. 24.
- 1848 Leptaena filosa (J. de C. Sowerby); Davidson, p. 318, pl. 3, fig. 9.
- 1848 Strophomena filosa (J. de C. Sowerby); Phillips and Salter, p. 380.
- 1871 Strophomena filosa (J. de C. Sowerby); Davidson, p. 307, pl. 45, figs. 14–20.
- 1892 Leptostrophia filosa (J. de C. Sowerby); Hall and Clarke, p. 288.
- 1963 Leptostrophia filosa (J. de C. Sowerby); Holland et al., pl. 3, figs. 3, 5,

Comparison. L. (L.) filosa differs from the common Upper Llandovery species L. (L.) compressa (J. de C. Sowerby) in being weakly concavo-convex to plano-convex and in having equally parvicostellate ornament, a more sharply triangular ventral muscle field with strong, relatively straight bounding ridges, and sub-parallel to weakly divergent cardinal process lobes and short socket plates. In L. (L.) compressa the convexity is rather variable, but is always stronger than in filosa; the ornament may vary from equally to unequally parvicostellate, the ventral muscle field has a broadly triangular outline and the bounding ridges are commonly weak and gently curved, and the cardinal process lobes and relatively long socket plates are widely divergent.

Description. Exterior. Very gently concavo-convex to plano-convex, commonly approaching biplanate condition; body cavity very narrow. Subquadrate to semicircular in outline, hinge-line straight, probably always forming point of maximum width, though delicate cardinal extremities frequently broken. Lateral margins of shell sub-parallel or gently curved, anterior margin rounded. Commissures smooth, anterior commissure rectimarginate.

Ventral interarea short, plane, apsacline. Delthyrium appears to be open (on material studied). Dorsal interarea plane, anacline. Notothyrium closed by convex chilidium. Ornament finely and equally parvicostellate with about 3 costellae per mm at 5-mm growth stage. Costellae low, rounded, straight along mid-line of shell but gently curved laterally. Surface of well-preserved specimens bears numerous fine, very closely spaced growth fila.

Interior of pedicle valve. Ventral process low, flat, narrow, slightly hollowed out along mid-length and produced anteriorly as slender myophragm which longitudinally bisects muscle field. Process pits narrow, elongated. Hinge-line denticulate for half its

length, denticles being borne on pair of short denticular plates. Minute hinge teeth may be present.

Muscle field sharply triangular in outline, well impressed, anteriorly flabellate, occupying about half to two-thirds of length of valve; bounded laterally by fairly strong ridges, commonly straight, but may be gently curved (medially convex). Bounding ridges arise immediately anterior to hinge, diverge antero-laterally at about 50° to one another, die out at about mid-length of muscle field, which remains unbounded anteriorly. Adductor scars narrow, elongate, separated by myophragm and extending anteriorly for just over half of length of muscle field. Diductor scars large, triangular, commonly scored by strong, radiating striae.

Area immediately lateral to muscle bounding ridges may be coarsely tuberculate and whole of internal surface is finely pseudopunctate.

Interior of brachial valve. Cardinalia supported on fairly high notothyrial platform. Cardinal process lobes narrow, plate-like, upright, sub-parallel, with attachment faces

EXPLANATION OF PLATE 57

Figs. 1-6. Leptostrophia (Leptostrophia) filosa (J. de C. Sowerby).

- 1a-c. Dorsal, ventral, and lateral views of articulated shell, NMW 70.3G.7, $\times 1.3$, top 10 ft of Wenlock Limestone, old quarry on W side of road from Cwm to Ton Farm, Usk inlier, Mon., SO/3325.0180.
- 2. Internal moulds of 3 pedicle valves, GSM 12755, \times 1, Wenlock Series, Llandovery district, Carms.; figured Davidson 1871, pl. 44, fig. 20.

3. Interior of pedicle valve, GSM 13306, ×1, Wenlock Limestone, Dudley, Worcs.

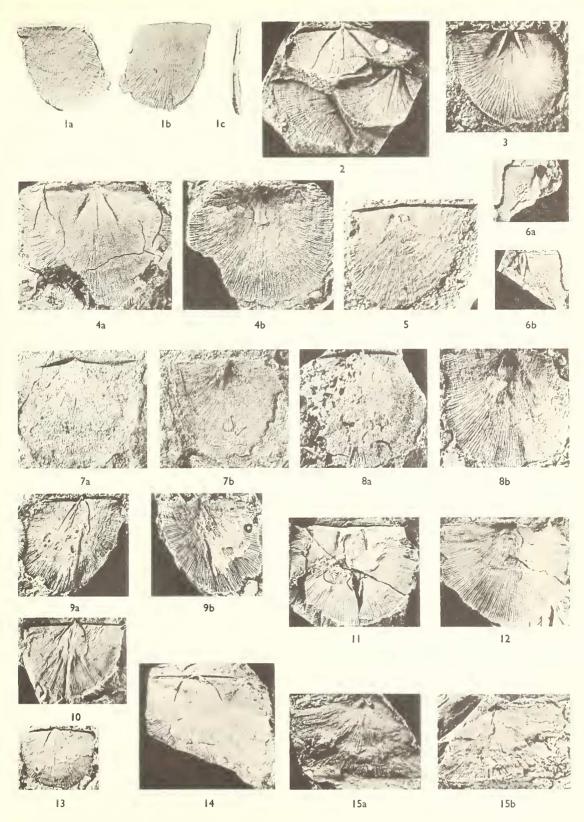
- 4a, b. Artificial (calcined) internal mould of pedicle valve and counterpart exterior, NMW 70.3G.8a, b, $\times 1.3$, locality and horizon as for fig. 1.
- 5. External mould of brachial valve, lectotype, GSM Geol. Soc. Colln. 6644, ×1·3, Wenlock Shale, Oldcastle, Malvern Hills.
- 6a, b. Internal mould of brachial valve and latex cast, NMW 70.3G.10, $\times 1.5$, siltstone overlying Wenlock Limestone, old quarry at Cwm, Usk inlier, Mon., SO/3331.0160.

Figs. 7, 8. Leptostrophia (Leptostrophia) compressa (J. de C. Sowerby).

- 7a, b. Internal mould of pedicle valve and counterpart external mould, UB 12376a, b, ×1, base of Wenlock Series, near hedgerow, approx. 280 yd SSE of Underwood Farm, Charfield, Tortworth inlier, Glos.
- 8a, b. Internal mould of pedicle valve and counterpart external mould, CMB Cb4608a, b, ×1, base of Wenlock Series, exposure in ditch, approx. 170 yd S.33°E. of Catherine Villa, Stone, Tortworth inlier, Glos.

Figs. 9-15. Mclearnites coralli sp. nov.

- 9a, b. Internal mould of pedicle valve and counterpart external mould, GSM 12753/4, \times 1, 'Wenlock Shale' (probably Coralliferous Series), Lindsway Bay, Pembs.
- 10. Internal mould of pedicle valve, holotype, GSM 12747, ×1, 'Wenlock Shale' (Coralliferous Series), Slate Mill, Hasguard, Pembs.
- 11. External mould of brachial valve showing interareas and part of ventral muscle field impressed by compression, GSM 12787, \times 1, locality and horizon as for fig. 10.
- 12. External mould of pedicle valve, GSM 12786, $\times 1$, locality and horizon as for fig. 10.
- 14. Internal mould of pedicle valve, SM A39419, ×1, 'Calcareous Grits, ? Ludlow' (probably Sandstone Series, late Wenlock), 130 ft above base of succession, Lindsway Bay, Pembs.
- 15a, b. Internal mould of brachial valve and latex cast, NMW 70.3G.36, \times 1, base of Sandstone Series (probably late Wenlock), cliff section, Marloes Bay, 430 yd SW of Little Marloes Farm, Pembs., SM/7880.0710.



BASSETT, Wenlock Stropheodontidae



directed slightly postero-ventrally. Socket plates sub-parallel to cardinal process lobes or only slightly divergent.

Muscle field well impressed, truncated oval in outline, bisected longitudinally by rounded ridge which represents an anterior continuation of notothyrial platform. Muscle field bounded laterally by pair of low, broad ridges; unbounded anteriorly. Semi-oval adductor scars occupy about a quarter of width of valve. Area immediately lateral to muscle field may be coarsely tuberculate.

Dimensions of figured specimens in mm

	Length	Width
Lectotype, GSM Geol. Soc. Colln. 6644	21.2	29·4 est.
GSM 13306	24.0	30·2 est.
GSM 13307	26.8	34.0 est.
GSM 12755		
NMW 70.3G.9a	21.2	25.5 est.
NMW 70.3G.7	17.4	
NMW 70.3G.8a, b	25.0	29.8
NMW 70.3G.10		
	GSM 13306 GSM 13307 GSM 12755 NMW 70.3G.9a NMW 70.3G.7	Lectotype, GSM Geol. Soc. Colln. 6644 21·2 GSM 13306 24·0 GSM 13307 26·8 GSM 12755 — NMW 70.3G.9a 21·2 NMW 70.3G.7 17·4 NMW 70.3G.8a, b 25·0

Type and figured specimens. Lectotype (here selected), GSM. Geol. Soc. Colln. 6644; J. de C. Sowerby in Murchison, p. 630, pl. 13, fig. 12; from the Wenlock Shale of 'Old Castle' in the Malvern Hills, one of the localities originally mentioned by Sowerby (op. cit., p. 630). This specimen is re-figured on Plate 57, fig. 5. It was presumably one of at least two specimens available to Sowerby as he also recorded the species from Burrington in the Ludlow anticline; however, the whereabouts of any syntypes apart from the lectotype are not known.

Distribution. This species occurs fairly commonly in the upper Wenlock Shale and in the Wenlock Limestone throughout the Welsh Borderland. It is not known from early Wenlock horizons and is known only rarely in the late Wenlock mudstones of the Llandovery–Llandeilo district. No specimens have been collected from Pembrokeshire. It is also a fairly common species in the early–middle Ludlow beds of the shelf area, being recorded by Lawson (1960, p. 119) as rare or absent after Leintwardinian times.

Leptostrophia (Leptostrophia) compressa (J. de C. Sowerby)

Plate 57, figs. 7, 8

1839 Orthis compressa J. de C. Sowerby in Murchison, p. 638, pl. 22, fig. 12.

1967 Leptostrophia (Leptostrophia) compressa (J. de C. Sowerby); Cocks, p. 248, pl. 37, figs. 1–9, 11 (see also for full synonymy).

Discussion. A number of specimens of L. (L.) compressa have been examined by the writer from the base of the Wenlock Series in the Tortworth inlier. They were collected by Dr. M. L. K. Curtis from beds of fine sandstone which he considers to be the lateral equivalents of the basal Wenlock limestone in other parts of the inlier. Cocks (1967, pp. 248–52) described the variation in Upper Llandovery specimens of compressa in great detail and as the basal Wenlock specimens fall within this range there is little need to describe them here.

Cocks (1967) showed that the mean angle of divergence of the ventral muscle field of L. (L.) compressa increases with time in the Upper Llandovery. Insufficient material has been available to determine whether the angle of the muscle divergence of an early Wenlock population may be distinguished from that in late Llandovery populations. In two Wenlock specimens examined by the writer the muscle divergence is about 100° , but this figure falls within the range recorded by Cocks for his youngest Llandovery (C_6) population.

L. (L.) compressa has also been recorded by Cocks (1967, p. 249) from sandstone lenses in the Woolhope Limestone, of basal Wenlock age, in the May Hill inlier.

Subgenus Leptostrophia (Eostropheodonta) Bancroft 1949

Type species. Orthis hirnantensis McCoy 1851, by original designation of Bancroft 1949, p. 9.

Discussion. The writer agrees with Cocks (1967, p. 247) that the plano-convex to gently concavo-convex subgenus Eostropheodouta is best regarded as a subgenus of Leptostrophia. Therefore, although assigned to the subfamily Stropheodontinae by Williams (1965, p. H395) Eostropheodouta is here removed to the Leptostrophiinae, Haylíček (1967, pp. 80, 81) recognized Eostropheodouta as a distinct genus which he assigned to a new family Eostropheodontidae. In reaching this conclusion Haylíček (1967) suggested that Eostropheodonta was derived from the rafinesquinids and differs from the true stropheodontids in lacking denticulation of the cardinal margin and in lacking a ventral process which separates process pits. However, as Williams (1953a, pp. 8-10) has convincingly demonstrated, even the earliest representatives of *Eostropheodonta*, including the type species E. hirnauteusis, possess primitive denticulate plates which became modified and reduced in the phylogenetic development of the stock, resulting in the eventual disappearance of dental plates and the spread of denticles along the hinge-line; this development also took place in other stropheodontid groups and there can be little doubt that it represented a real phylogenetic trend in the family as a whole. Similarly Williams (1953a, pp. 13-15) indicated that the ventral process of stropheodontids became more pronounced with time and its weak development or absence in the earliest representatives does not justify the recognition of a separate family. Havlíček's family Eostropheodontidae is therefore not recognized here, although the writer agrees that Eostropheodonta itself was probably derived from a rafinesquinid ancestor. As discussed above, Eostropheodonta is regarded instead as an early member of the leptostrophiid stock.

Cocks (1967, p. 247) demonstrated that Llandovery specimens of *Eostropheodonta*, which possess dental plates, may occur contemporaneously with related specimens of *Leptostrophia* s.s., which lack dental plates. The description below of a Wenlock species of *Eostropheodonta* indicates that this type of coexistence continued into the Wenlock period.

 $Leptostrophia\ (Eostropheodonta)\ {\rm sp.}$

Plate 56, figs. 7, 8

Description. Exterior of pedicle valve. Valve gently convex at umbo but almost flat for remainder of length. Outline subquadrate, hinge-line straight with very short, rounded

ears. Lateral margins sub-parallel, anterior margin evenly curved. Anterior commissure rectimarginate.

Ventral interarea very weakly apsacline. Delthyrium triangular, apparently open. Fine, parallel growth-lines visible on the interarea.

Ornament unequally parvicostellate with up to 4 fine costellae occupying interspaces between low, rounded major costellae. Median costellae straight, lateral costellae gently curved. Whole surface crossed by very fine, slightly lamellose growth fila.

Interior of pedicle valve. Very short, slender dental plates diverge antero-laterally at about 90–100° to one another. Small callist occupies posterior part of delthyrial cavity. Two short, flat plates on hinge-line immediately alongside delthyrium probably represent denticular plates.

Musculature obscure but muscle field appears to have broadly triangular outline and lacks bounding ridges. Internal surface strongly impressed by external ornament.

Brachial valve unknown.

Dimensions of figured specimens in mm

		Length	Width
Internal mould of pedicle valve and			
counterpart external mould	NMW 70.3G.11a, b	19.3	21.0 est.
External mould of pedicle valve	NMW 70.3G.12 <i>b</i>	20.6	_

Distribution. The above description is based on 3 poorly preserved external and internal moulds of pedicle valves from the Wenlock Shale of Craig-y-Garcyd in the Usk inlier, Monmouthshire (Grid. Ref. SO/3570.0275). The specimens are slightly flattened and no denticles have actually been observed because of the resulting poor preservation. However, the distinctive parvicostellate ornament and the presence of what are probably denticular plates clearly indicate the stropheodontid affinities of the specimens.

Subfamily DOUVILLININAE Caster 1939 Genus Amphistrophia Hall and Clarke 1892 Subgenus *Amphistrophia* (*Amphistrophia*) Hall and Clarke 1892

Type species, Strophomena striata Hall 1843, by original designation of Hall and Clarke 1892, p. 292.

The subgenus *Amphistrophia* (*Amphistrophia*) is here restricted to include only those amphistrophiids which lack dental plates. A new subgenus, *Amphistrophia* (*Pembrostrophia*), is erected (see p. 325) to include forms with dental plates.

Amphistrophia (Amphistrophia) whittardi Cocks

Plate 58, figs. 2-4

1932 Stropheodonta funiculata (McCov); Whittard, list facing p. 896.

1967 Amphistrophia whittardi Cocks, p. 261, pl. 39, figs. 3, 5, 8.

Comparison. This species closely resembles A. (A.) funiculata (McCoy) in outline and convexity but the two are easily distinguished by differences in musculature and ornamentation. A. (A.) whittardi has unequally parvicostellate radial ornament and weakly

impressed muscle fields which lack well-developed bounding ridges. In contrast A. (A.) funiculata has equally or subequally parvicostellate ornament and well-impressed ventral and dorsal muscle fields, both of which are bounded by strong ridges.

Description. Exterior. Semicircular to semi-elliptical in outline, about two-thirds as long as wide. Shell resupinate; pedicle valve initially gently convex, brachial valve initially gently concave. At about five-sixths of valve length both valves are geniculated smoothly and fairly gently in ventral direction. Hinge-line straight, slightly mucronate, forming point of maximum width of shell. Lateral margins evenly curved, anterior margin gently curved or prolonged slightly anteriorly to produce subtriangular outline. Anterior commissure rectimarginate.

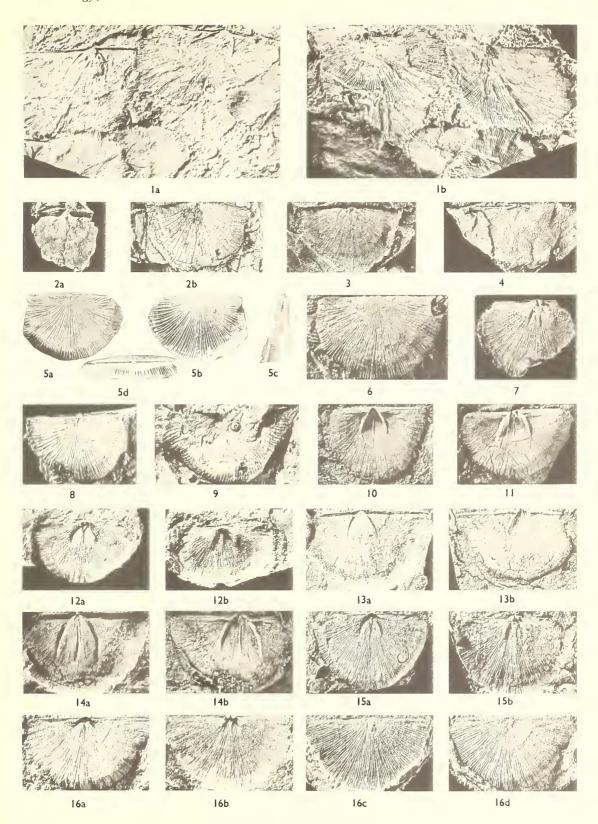
Ventral interarea plane, apsacline. Delthyrium bears small, apical pseudodeltidium; delthyrial angle about 90°. Dorsal interarea plane, anacline. Notothyrium occupied by cardinal process.

Ornament unequally parvicostellate. Three or four fine costellae occupy broad interspaces between larger, rounded, major costellae.

Interior of pedicle valve. Ventral process low, flat. Dental plates absent. Pair of low denticular plates occupy median third of hinge. Muscle field weakly impressed, individual

EXPLANATION OF PLATE 58

- Figs. 1a, b. Mclearnites coralli sp. nov. Internal and external moulds of pedicle valves showing the typical distorted preservation, NMW 70.3G.37a, b, ×1, base of Sandstone Series (probably late Wenlock), cliff section, Marloes Bay, 430 yd SW of Little Marloes Farm, Pembs., SM/7880.0710.
- Figs. 2-4. Amphistrophia (Amphistrophia) whittardi Cocks.
 - 2a, b. Internal mould of pedicle valve and counterpart external mould, NMW 70.3G. 33a, b, $\times 1.5$, Wenlock mudstone, W bank of Afon Sawdde, 500 yd SE of Rhydsaint, Carms., SN/7182.2551.
 - 3, 4. Internal moulds; 3, pedicle valve, NMW 70.3G.34, $\times 1.5$; 4, brachial valve, NMW 70.3G. 35a, $\times 1.5$, locality and horizon as for fig. 2.
- Figs. 5–16. Amphistrophia (Amphistrophia) funiculata (McCoy).
 - 5 a-d. Dorsal, ventral, lateral, and posterior views of complete shell, NMW 70.3G.13, ×1·5, Wenlock Limestone, old quarry and tip on W side of Lincoln Hill, Ironbridge, Salop., SJ/6695.0381.
 - 6, 7, 8. Brachial valves; 6, exterior, NMW 70.3G.14, $\times 1.5$; 7, interior, NMW 70.3G.15, $\times 2$; 8, exterior, NMW 70.3G.16, $\times 2$; locality and horizon as for fig. 5.
- 9. External mould of pedicle valve, lectotype, NMI 111 11, ×1·5, Silurian, Doonquin, Dingle, Co. Kerry, Ireland.
- 10, 11. Interiors of pedicle valves; 10, NMW 70.3G.17, $\times 1.5$; 11, NMW 70.3G.18, $\times 1.5$, locality and horizon as for fig. 5.
- 12a, b. Internal mould of brachial valve and latex cast, NMW 70.3G.19, ×1·5, siltstone overlying Wenlock Limestone, old quarry at Cwm, Usk inlier, SO/3331.0160.
- 13*a*, *b*. Internal mould of pedicle valve and latex cast, NMW 70.3G.20, ×1·5, Wenlock Shale, temporary drainage trench from Cwm to railway line at Monkswood, Usk inlier, Mon., SO/3335. 0173 to 3371.0215.
- 14a, b. Internal mould of pedicle valve and latex cast, NMW 70.3G.21a, $\times 1.5$, locality and horizon as for fig. 12.
- 15a, b. Internal mould of brachial valve and latex cast, NMW 70.3G.22a. $\times 1.5$, locality and horizon as for fig. 12.
- 16 a-d. Internal mould of brachial valve and latex cast, counterpart external mould and latex cast, NMW 70.3G.23a, b, $\times 1.5$, locality and horizon as for fig. 13.



BASSETT, Wenlock Stropheodontidae



scars not discernible. Very faint myophragm bisects muscle field longitudinally. Extremely short, faint ridges arise near umbo and diverge antero-laterally at about 90° to one another to bound muscle field postero-laterally; these ridges die out rapidly and greater proportion of muscle field remains unbounded.

Interior of brachial valve. Notothyrial platform very low. Cardinal process lobes subparallel, postero-ventrally directed. Sockets shallow, elongated; socket plates low, fairly wide, antero-laterally divergent at about 120° to one another. Muscle field not impressed, bounding ridges absent.

Dimensions of figured specimens in mm

		Length	Width
Internal mould of pedicle valve and		_	
counterpart external mould	NMW 70.3G.33a, b	11.2	18.6
Internal mould of pedicle valve	NMW 70.3G.34	11.9	16.7
Internal mould of brachial valve	NMW 70.3G.35a	11.7	_

Type and figured specimens. The specimens of A. (A.) whittardi figured by Cocks (1967, pl. 39, figs. 3, 5, 8), including the holotype, are in the Oxford University Museum (see Cocks, 1967, p. 262).

Distribution. This species has been collected by the writer from a single locality in the Sawdde gorge section, Carmarthenshire (Grid. Ref. SN/7176.2562) in beds mapped by Williams (1953b, p. 198) as lower Wenlock in age. It was previously recorded by Cocks (1967, p. 263) only from the late Llandovery Purple Shales of the Welsh Borderland, but has also been examined by the writer in collections, now housed in the City Museum, Bristol, made by Dr. M. L. K. Curtis from the Upper Llandovery of the Tortworth inlier.

Amphistrophia (Amphistrophia) funiculata (McCoy)

Plate 58, figs. 5-16

- 1846 Orthis funiculata McCoy, p. 30, pl. 3, fig. 11.
- 1847 Leptaena funiculata (McCoy); Davidson, p. 57, pl. 12, figs. 5–8.
- 1848 Leptaena fuuiculata (McCoy); Davidson, p. 317, pl. 3, fig. 5.
- 1852 Leptaena (Strophoniena) funiculata (McCoy); McCoy, p. 244.
- 1861 Strophomena funiculata (McCoy); Lindström, p. 372.
- 1871 Strophomena funiculata (McCoy); Davidson, p. 290, pl. 40, figs. 9–13.
- 1963 Strophonella funiculata (McCoy); Holland et al., pl. 3, figs. 5, 6, 7.
- ? 1967 Amplistrophia funiculata (McCoy); Havlíček, p. 186, pl. 29, figs. 1, 2, 4, 5, 9.

Discussion. McCoy's (1846, pl. 3, fig. 11) original specimen of 'Orthis' funiculata, from the Silurian of Doonquin, Dingle, Co. Kerry, Ireland, is an extremely poorly preserved external mould of a pedicle valve. The antero-lateral margins of this shell have a rather angular outline in comparison with the evenly curved margins of specimens from the Welsh Borderland and neighbouring areas which are commonly identified as funiculata. Unfortunately material from Dingle is very rare so it is not possible to judge at this stage whether the difference in shape between the lectotype and Anglo-Welsh shells is taxonomically significant. However, three poorly preserved specimens of funiculata, collected from Dingle by Professor C. H. Holland, show some variation in outline and

have ventral muscle fields which are morphologically inseparable from those in Anglo-Welsh specimens. It seems advisable, therefore, to retain the name *funiculata* for the latter. If future studies should indicate that populations from Dingle have a significantly different shape, the differences will probably be best expressed by splitting off the Anglo-Welsh shells at no more than the subspecies level.

Comparison. A comparison of this species with A. (A.) whittardi is given earlier (p. 319). A. (A.) funiculata differs from A. (A.) striata (Hall), the type species of Amphistrophia from the Waldron Shale of Indiana, in having a transversely semicircular outline, a relatively longer ventral muscle field which may be completely bounded by ridges, and in being fairly sharply geniculate. A. (A.) striata has a subquadrate outline, is only gently resupinate, and has a ventral muscle field which is confined to the posterior half of the valve and is unbounded anteriorly.

Description. Exterior. Outline semicircular to semi-elliptical, commonly about two-thirds to half as long as wide. Maximum width at straight hinge-line, which may be produced as short rounded ears. Shells resupinate; pedicle valve initially gently convex, brachial valve initially gently concave. Valves are then geniculated fairly sharply ventrally, commonly between 10- and 15-mm growth stages. Commissures crenulate, anterior commissure rectimarginate. Ventral interarea plane, apsacline, about 3 times as long as dorsal interarea which is plane, anacline. Delthyrium bears small, convex, apical pseudodeltidium and is partially occupied by cardinal process. Delthyrial angle about 80°. Notothyrium filled by cardinal process, which is flanked by pair of slender chilidial plates. Impress of internal denticulation may be visible on both interareas. Ornament equally to sub-equally parvicostellate with 4–5 low, rounded costellae per mm at 10-mm growth stage. New costellae arise both by insertion and bifurcation.

Interior of pedicle valve. Ventral process low, produced anteriorly as slender myophragm which longitudinally bisects muscle field. Process pits shallow. Median third of hinge denticulate, denticles being borne on pair of well-defined denticular plates.

Muscle field strongly impressed, longitudinally oval in outline, occupying from half to four-fifths of total length of valve. Strong, medially concave ridges bound muscle field laterally, and may die out at point where muscle field reaches maximum width in its anterior half; muscle field may then remain unbounded anteriorly; in some specimens bounding ridges completely enclose muscle field, intersecting myophragm at its anterior extremity. Adductor scars narrow, lanceolate, confined to posterior half of muscle field and bounded laterally and anteriorly by large, oval diductor scars.

Internal surface may be coarsely tuberculate and may show impress of external ornament.

Interior of brachial valve. Cardinal process lobes postero-ventrally directed, U-shaped in cross-section, pear-shaped in outline, separated medially by rounded groove. Sockets fairly deep, bounded anteriorly by strong socket plates diverging antero-laterally at about 100–120° to one another and which may be crenulated on their posterior edges.

Muscle field well impressed, truncated oval in outline, occupying about one-quarter of length of valve. Adductor scars bounded laterally by strong, medially concave ridges;

unbounded anteriorly. Muscle scars separated longitudinally by low, rounded myophragm arising below the cardinalia and tapering anteriorly.

Area immediately lateral to muscle field commonly coarsely tuberculate.

Dimensions of figured specimens in mm

est.
est.
est.
est.
est.
est.

Type specimens. Lectotype (here selected, figured McCoy 1846, pl. 3, fig. 11), NMI 111 11. It is refigured on Plate 58, fig. 9. This is one of 2 specimens that were available to McCoy from the collection of Sir Richard Griffith; the other specimen is also in the National Museum of Ireland but is unregistered.

Distribution. A. (A.) funiculata occurs very commonly in the upper Wenlock Shale and the Wenlock Limestone throughout the Welsh Borderland and less commonly in the late Wenlock sandstones and mudstones of Tortworth and South Wales. It is not known from Pembrokeshire and does not occur in beds of early Wenlock age. The species ranges through into the Ludlovian where it is recorded by Lawson (1960, p. 117) as being rare or absent after Bringewoodian times. On Gotland it is recorded by Hede (1960) from localities in the Slite and Mulde Marls; both of these divisions are considered to be of Wenlock age.

Amphistrophia (Amphistrophia) cf. euglyphoides Holtedahl
Plate 59, figs. 1-4

cf. 1916 Amphistrophia euglyphoides Holtedahl, p. 65, pl. 6, figs. 7-9.

Comparison. A few poorly preserved specimens examined by the writer from the base of the Wenlock succession in the Tortworth inlier closely resemble A. (A.) euglyphoides Holtedahl in details of shape, convexity, ornament, and configuration of the ventral muscle field. However, until well-preserved specimens, including dorsal interiors, are collected from Tortworth, the comparison with euglyphoides must remain tentative. The pedicle valves of A. (A.) euglyphoides figured by Holtedahl (1916, pl. 6, fig. 8) are refigured for comparison on Plate 59, fig. 5.

A comparison of A. (A.) cf. euglyphoides and A. (P.) freshwaterensis is given on p. 326.

Description. Exterior. Shell resupinate, gently concavo-convex initially, becoming gently convexi-concave after length of about 10 mm. Outline subquadrate, hinge-line

straight, cardinal angles rounded. Lateral margins sub-parallel, straight to gently curved, anterior margin evenly rounded.

Ventral interarea apsacline, dorsal interarea anacline. Nature of delthyrium and notothyrium not observed.

Radial ornament fine, equally parvicostellate with approximately 4–5 low, rounded costellae per mm at 5-mm growth stage.

Interior of pedicle valve. Ventral process flat, produced anteriorly as very slender myophragm. Muscle field sub-oval, confined to posterior half of valve and occupying about one-third of valve width. Individual scars not discernible. Low, gently curved ridges bound muscle field laterally, but unbounded anteriorly where margin may be slightly flabellate.

Interior of brachial valve. Unknown.

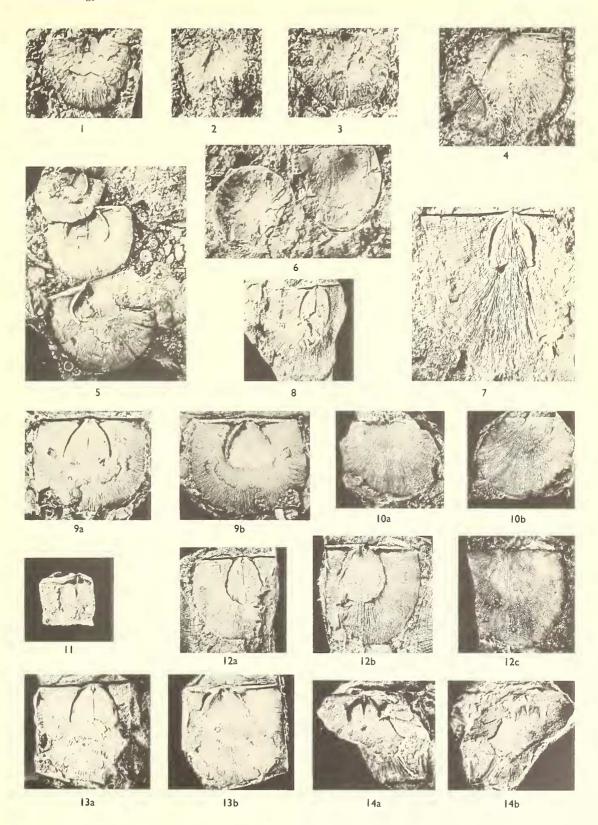
Dimensions of figured specimens in mm

	Length	Width
GSM DEW9543A	22.5	28·0 est.
GSM DEW9543B	16.1	19·1 est.
GSM DEW9548		_
CMB Cb4610	15.0	17.9
	GSM DEW9543B GSM DEW9548	GSM DEW9543A 22:5 GSM DEW9543B 16:1 GSM DEW9548 —

Distribution. A (A.) cf. euglyphoides is known only from the Tortworth inlier where it occurs rarely in the limestone band at the base of the Wenlock Series and in sandstone

EXPLANATION OF PLATE 59

- Figs. 1-4. Amphistrophia (Amphistrophia) cf. euglyphoides Holtedahl.
 - 1. Exterior of brachial valve, CMB Cb4610, × 1·3. Wenlock Series, Whitfield, Tortworth inlier, Glos.
 - 2, 4. Interiors of pedicle valves; 2, GSM DEW9548, ×1·3; 4, GSM DEW9543A, ×1·5; basal Wenlock limestone, Rifle Cottage Quarry, Tortworth inlier, Glos.
 - 3, Exterior of brachial valve, GSM DEW9543B, ×1·3, locality and horizon as for fig. 2.
- Figs. 5–6, Amphistrophia (Amphistrophia) euglyphoides Holtedahl.
 - 5. Interiors of pedicle valves, PMO L0116, \times 1, Stage 9c, Langø, off Holmestrand, Oslo district, Norway; figured Holtedahl 1916, pl. 6, fig. 8.
 - 6. Exteriors of pedicle valves, PMO L0122, ×1, locality and horizon as for fig. 5; figured Holtedahl 1916, pl. 6, fig. 7.
- Fig. 7. Amphistrophia (Amphistrophia) sp. Internal mould of pedicle valve, GSM Hc992, XI, late Wenlock mudstone, old overflow trench near Middleton Hall, Carms., SN/5265.1879.
- Fig. 8. Amphistrophia sp. Internal mould of pedicle valve, NMW 70.3G.47, ×1, base of Sandstone Series (probably late Wenlock), cliff section above Marloes Bay, approx. 750 yd NW of Little Marloes Farm, Pembs., approx. SM/7835.0765.
- Figs. 9–14. Amphistrophia (Pembrostrophia) freshwaterensis subgen. et sp. nov. Top of Wenlock (of Dixon 1921), large reef on beach approx. 30 ft above lowest beds, S side of Freshwater East Bay, Pembs., SS/0165.9753.
 - 9a, b. Internal mould of pedicle valve and latex cast, holotype, NMW 70.3G.25, $\times 1.25$.
 - 10a, b. External mould of brachial valve and latex cast, NMW 70.3G.26, $\times 1$.
 - 11. Internal mould of brachial valve, NMW 70.3G.27, \times 1.5.
 - 12 a–c. Internal mould of brachial valve, latex cast, and counterpart external mould, NMW 70. 3G.28a, b; a, \times 1; b, c, \times 1·25.
 - 13a, b. Internal mould of pedicle valve and latex cast, NMW 70.3G.29, $\times 1.25$.
 - 14a, b. Internal mould of brachial valve and latex cast, NMW 70.3G.30, $\times 1.25$.



BASSETT, Wenlock Stropheodontidae



beds which are considered by Dr. M. L. K. Curtis to be lateral equivalents of the basal limestone in some parts of the inlier.

Amphistrophia (Amphistrophia) sp.
Plate 59, fig. 7

A single specimen of *Amphistrophia* in the collections of the Geological Survey Museum (GSM Hc992), from the late Wenlock of Middleton Park, Carmarthenshire, differs from any other specimen described here mainly in its large size and longitudinally elongated outline. Associated with the specimen is a brachial valve which may belong to the same species. A full description of this species is deferred until more material can be collected to allow its relationships with other species to be assessed.

Dimensions in 11111. Length, 41.7; width 46.0 est.

Subgenus Amphistrophia (Pembrostrophia) subgen. nov.

Type species. Amphistrophia (Pembrostrophia) freshwaterensis sp. nov.

Diagnosis. A subgenus of Amphistrophia possessing dental plates.

Discussion. In the late Wenlock/Ludlow rocks of Freshwater East Bay, Pembrokeshire, there occurs a fairly large gently resupinate amphistrophiid which possesses small but distinctive dental plates and which thus morphologically represents the 'Eo' stage (Williams 1953a, p. 30) of Amphistrophia s.s. As the earliest species of Amphistrophia yet recorded is A. (A.) whittardi from the late Llandovery of the Welsh Borderland (Cocks 1967, p. 262) one would normally expect 'Eo' forms of the genus to occur in beds of pre-Upper Llandovery age. The presence of amphistrophiids with dental plates in Wenlock/ Ludlow rocks is therefore somewhat surprising. If it is assumed that Amphistrophia followed the normal pattern of stropheodontid evolution, and that forms with dental plates ('Eo' stage) gave rise to forms without dental plates ('Meso' stage), the Pembrokeshire specimens described here may be considered to represent conservative members of an ancestral amphistrophiid stock existing contemporaneously with descendant forms. In other respects, however, A. (P.) freshwaterensis appears to represent a fairly welladvanced species since it has patterns of ribbing and musculature more closely comparable with those in A. (A.) funiculata than in the early species A. (A.) whittardi; there is a possibility, therefore, that A. (P.) freshwaterensis developed from a stock without dental plates and that these structures were introduced as a secondary phenomenon, perhaps in response to local environmental conditions.

It is interesting to note that within one population of A. (P.) freshwaterensis the development of dental plates is rather variable and in a few specimens they are represented instead by low flat pads of shell material (e.g. Pl. 59, fig. 13). If the presence of plates is explained purely in evolutionary terms then it is probable that the species is approaching the stage where plates will be completely lost. Some support for this alternative is provided by a few specimens of Amphistrophia collected from low in the Sandstone Series of Marloes Bay in Pembrokeshire; these specimens are probably slightly younger